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Characterizing natural intervals of development in the early life of fishes: an example using blennies (Teleostei: Blenniidae)

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Abstract

We examined patterns and timing of ontogeny in five species of blenny (Teleostei: Blenniidae) from the northern Gulf of Mexico by assigning a suite of discrete character scores to individual ontogenetic events (10 external characters; 218 specimens). Our approach applies scaling techniques and statistical methods to quantify, differentiate, and select criteria to delimit intervals of development across taxa. We consistently identified three natural intervals of development (labeled 'Larvae', 'Metamorphs', and 'Settlers'). Larvae had total character scores ≤ 13 and ontogenetic index (O_L) values <80. Metamorphs had total character scores from 15 to 30, and O_L values from 80 to 90.3. Settlers had total character scores ≥ 25 and O_L values ≥ 83. State of orbital cirrus and fin development, number of teeth, and body pigmentation patterns provided most of the power to discriminate intervals. We recommend the use of numerous, general (not species-specific), and diverse (i.e., morphological, behavioral, physiological, pigmentation, etc.) characters to delineate intervals of development, but especially fin ontogeny and dentition. Assignment of character scores to discrete ontogenetic events, when combined with a dimensionless index permits quantification of the timing of ontogeny, identification of the events that delimit intervals of development, and interspecific comparison. The diversity of teleosts and their life-history patterns may prohibit development of a standardized staging system across higher taxonomic levels, but standardization at the family level appears possible.

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Introduction

The complex life cycle of many marine fishes consists of intervals of development, each interconnected but with different growth and survival requirements and population dynamics (Hempel 1965; Frank and Leggett 1994). Objective characterization of intervals is crucial for examination of factors that influence survival and year-class strength because these processes may be interval-specific (Richards and Lindeman 1987; Kingsford 1988; Noakes and Godin 1988). Insight into developmental processes requires knowledge of the timing and synchronization of ontogenetic change (McCormick 1993; Higgs and Fuiman 1998). Poorly defined characters and lack of precise information on the position of a character within a developmental sequence have weakened attempts to delimit intervals in bony fishes (Ahlstrom 1968; Youson 1988; Fuiman and Higgs 1997). In fact, what appear to be similar characters are often used to describe completely different intervals (see Kingsford 1988) and sometimes multiple intervals (Gorodilov 1996). The wide variety of criteria and characters used to delimit intervals, the common misuse of developmental terminology, and the myriad of descriptive names that depict intervals has restricted our understanding of developmental processes.

Many aspects of development vary with an individual's size and/or age across species. These differences require a dimensionless metric that accounts for non-linear rates of ontogeny in order to make interspecific comparisons (Dettlaff and Dettlaff 1961; Fuiman et al. 1998). Customarily, length or age has been the reference point for interspecific comparisons. While length is an adequate basis for an index that permits intraspecific comparisons, length is not as effective in interspecific comparisons because genetic and environmental factors can induce size differences at comparable states of ontogeny that confound interspecific comparisons (Dettlaff and Dettlaff 1961; Fuiman and Higgs 1997; Fuiman et al. 1998).

Recent advances in developmental scaling methods (Fuiman 1994; Fuiman et al. 1998) permit comparison of larvae of different species and evaluation of differences in the timing and synchrony of developmental events. 'Ontogeny,' as defined here, is the change (either progressive or regressive) in character state (i.e., morphological, behavioral, physiological, pigmentation, etc.), the appearance of new characters, or the loss of existing characters. The ontogenetic index (O_L) of Fuiman (1994) expresses the state of ontogeny of a larva at any point in a developmental sequence ($O_L = \log L/\log L_{juv} \cdot 100$) as a proportion of a logarithmic developmental sequence, where L = standard length (SL) and L_{juv} = SL at the beginning of the juvenile stage for a given species. Using L_{juv} to formulate the ontogenetic index corrects for differences in size at a given comparable state of ontogeny among taxa. We demonstrate a new methodological approach to delimit natural intervals of development in fishes by employing quantitative characters and objective statistical treatment of those characters. This methodology can be used to characterize an individual's state of ontogeny, group individuals into comparable intervals of development, and facilitate interspecific comparisons on a common, dimensionless scale.

Materials and Methods

Light trap collections from oil and gas platforms off Louisiana over a three-year period (1995-1997) contained five species of blenny, including tessellated blenny (*Hypsoblennius invemar*), freckled blenny (*Hypsoblennius ionthas*), *Hypleurochilus multifilis* (no common name), seaweed blenny (*Parablennius marmoreus*), and molly miller (*Scartella cristata*), all in the tribe Parablenniini, according to Bock and Zander (1986). Settlers were hand-netted over oyster shell reefs and along rock jetties; collected with slurp guns along the legs of oil and gas platforms; and gathered following explosive removal of oil and gas platforms. Specimens were fixed in 10% formalin and transferred to 70% ETOH after 24 h. Each data set contained a nearly continuous size series of specimens with only minor gaps in SL.

We examined 55-*Hypsoblennius invemar*, 42-*H. ionthas*, 41-*Hypleurochilus multifilis*, 50-*Parablennius marmoreus*, and 30-*Scartella cristata*. Each specimen was scored for a suite of characters with each score representing a discrete ontogenetic event or character state (Table 1). We use the term 'state' to designate an instantaneous position within an ontogenetic sequence. 'Stage' represents an interval of development as traditionally defined in early life history literature. Dipping specimens into a solution of Cyanine Blue 5R stain, also known as Acid Blue 113 (Saruwatari et al. 1997), improved the contrast of anatomical structures, such as sensory pores, fin rays, and cephalic cirri. Scores for individual characters were summed to produce a 'total character score' for each individual, with total scores ranging from 1 to 42 for the suite of characters used.

Assigning individuals to intervals of development with confidence requires methods that reduce ambiguity. We performed a cluster analysis on the total character scores for the species-pooled data set using complete linkage and Manhattan distance rules to organize and map group structure (James and McCulloch 1990). A minimum linkage distance of 20% separated major clusters. Cluster analysis attempts to find the best solution to classify cases into groups even when data lack clear group structure (DePatta Pillar 1999). Consequently, cluster stability requires a method to test partition strength (James and McCulloch 1990). We used the bootstrap resampling method of DePatta Pillar (1999) with 1000 iterations to test cluster stability, to determine the probability distribution, and to obtain nonparametric estimates of standard error. If clusters are stable, random variability between clusters should exceed variability within clusters. Accordingly, failure to reject the null hypothesis of stable group structure for the proposed number of clusters is consistent with group stability at the suggested confidence level of $\alpha = 0.10$ (DePatta Pillar 1999). We assigned resultant clusters descriptive labels, but do not imply support for any particular hierarchical terminology. After assigning individuals to an interval of development, a Discriminant Function Analysis (DFA) performed on the species-pooled scores for the 10 characters provided the interspecific criteria that discriminated intervals.

Results

Analysis of total character scores revealed three primary clusters or intervals of development (Figs. 1 and 2). Bootstrap resampling of data at the three-cluster level failed to reject the null hypothesis of group stability ($p > 0.15$); therefore, each cluster was assigned a descriptive label. One cluster, termed 'Larvae,' contained specimens with total character scores ≤ 13 and O_L values <80. A second

Table 1. Character states used to score the young of five species of blenny from the northern Gulf of Mexico. Each character state represents a separate ontogenetic event.

Score	Dorsal fin rays
0	Finfold, fin base thickening, or anlag only
1	Initial segmentation of earliest developing ray
2	Terminal ray of fin initially segmented
3	Pigment along shaft of at least one ray
4	Pigment along shaft of all rays
5	Consolidation of pigment into stripes, bars, or bands
	Caudal fin
0	Preflexion
1	Initial segmentation of earliest developing primary caudal ray
2	All primary rays initially segmented; secondary rays thickening
3	All rays formed (primary and secondary)
4	All primary rays with pigment along shaft
5	Initial bifurcation of any primary ray
	Body pigmentation pattern [1]
0	No trunk pigment laterally (excludes visceral mass and pectoral fins)
1	Proliferation of head pigment, especially above hindbrain and along operculum
2	Epidermal pigment behind nape (initial formation of first band of trunk pigment)
3	Two or more bands of pigment forming dorsolaterally along trunk
	Pectoral fin
0	Finfold or incipient rays only
1	Initial segmentation of earliest developing ray
2	All rays initially segmented
3	New epidermal pigment present on pectoral axil, rays, or fin membrane
4	Reduction in original pectoral fin pigmentation (fin initially pigmented) [2]
5	Complete loss of original pectoral fin pigmentation pattern (All rays pigmented) [2]
	Pelvic fin pigment
0	Absent
1	Usually a single melanophore midway along shaft of ray or on membrane between rays
2	Loss of aforementioned melanophore; pigment now scattered over pelvic fin base and basal portion of shaft
	Orbital cirrus
0	Absent or thickening nub without free distal margin
1	Distal margin free, filamentous, and unpigmented; may be furcate
2	Cirrus lightly pigmented; may be multiply furcate
	Nasal cirrus
0	Absent or thickening nub without free distal margin
1	Distal margin free, filamentous, and unpigmented; may be furcate
2	Cirrus lightly pigmented; may be multiply furcate

(Table 1 continued)

Score	Number of teeth
0	6 or fewer
1	8–10
2	12–14
3	16–18
4	20–22
5	24 or more
	Extent of bony ossicle formation along upper portion of lateral line
0	Anterior to 3 rd dorsal spine
1	Terminates between 3 rd and 6 th dorsal spines
2	Terminates between 6 th and 9 th dorsal spines
3	Beyond 9 th dorsal spine
	Longest preopercular spine relative to orbit diameter
0	Increase in spine length
1	Decrease in spine length
2	Longest spine nub-like or entirely resorbed
	Type of teeth [3]
0	Villiform teeth only
1	Mixed villiform and 'spade-shaped' incisiform teeth
2	Incisiform teeth (except posterior-most), minor changes in tooth shape hereafter
	Dorsal spines [3]
0	Finfold or anlag
1	Formation of less than 50% of spines
2	All spines formed and structurally distinct

[1] See text for explanation of differences in pigmentation patterns between *Parablennius marmoreus* and the other four species

[2] Opposite fin pigmentation pattern. Young *Parablennius marmoreus* lack pectoral fin pigment until just before settlement

[3] Characters included in total character state score but not analyzed further

cluster (termed 'Metamorphs') included specimens with total character scores that generally ranged from 15 to 30. Metamorphs had O_L values between 80 and 90.3. A third cluster, labeled 'Settlers,' contained specimens with total character scores ≥ 25, and O_L values ≥ 83. Settlers were collected from a demersal habitat (Table 2). The term larvae as commonly defined includes both our Larvae and Metamorphs categories, which are artificial labels assigned for convenience (Table 3).

Discrimination of interspecific intervals of ontogeny was achieved in the species-pooled data set. Two canonical roots extracted all variability between intervals ($p < 0.0001$; Fig. 1B; Table 3).

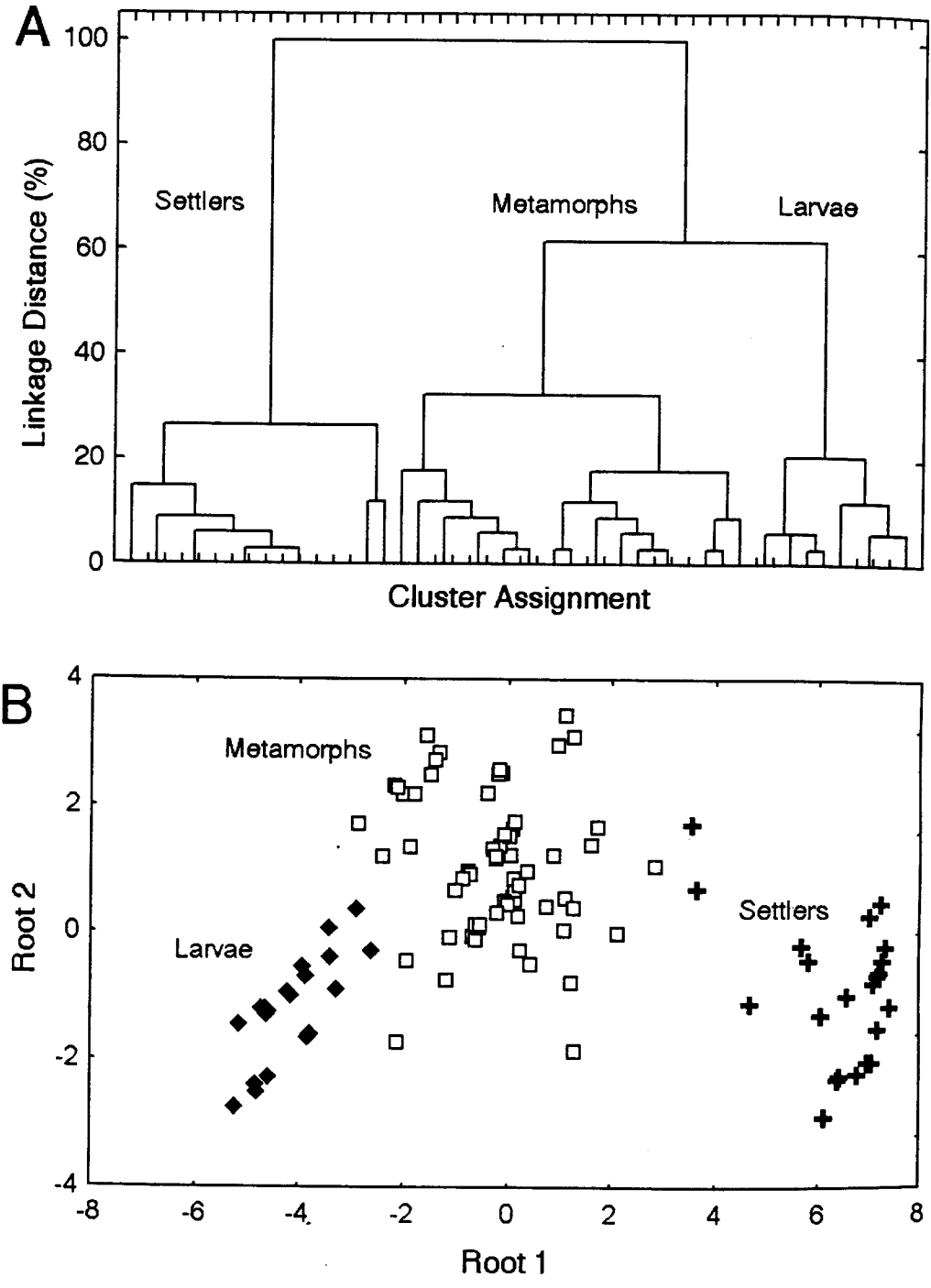

Figure 1. Intervals of development for the pooled data set of five species of blenny from the northern Gulf of Mexico. A. Typical cladogram from cluster analysis. B. Intervals of development as recognized by discriminant function analysis.

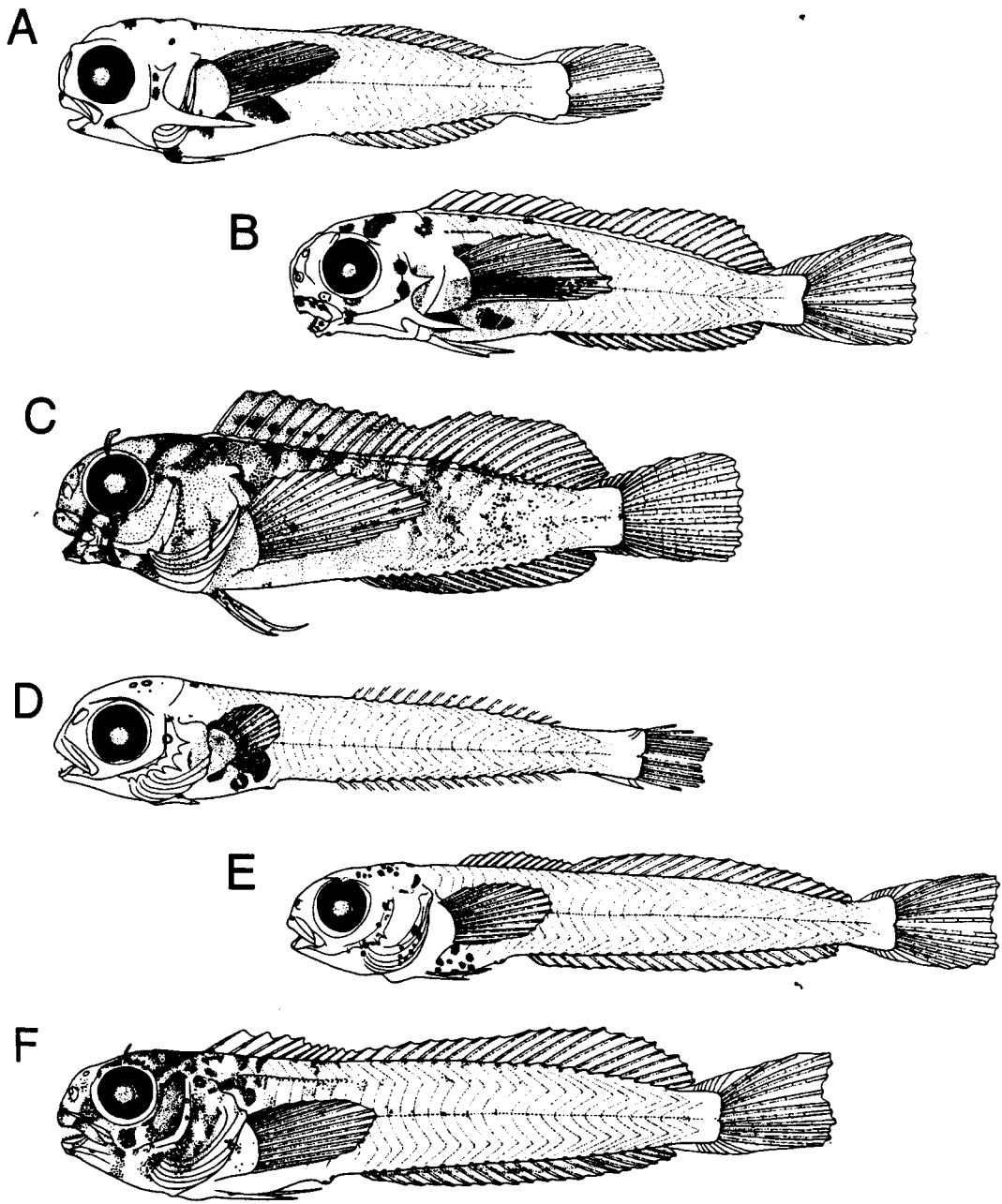

Figure 2. Early life stages of Hypsoblennius ionthas *(A-C) and* Parablennius marmoreus *(D-F) from the northern Gulf of Mexico. A. 5.4-mm; B. 10.2-mm; C. 11.8-mm; D. 5.8-mm; E. 13.7-mm; F. 17.3-mm (standard length). Larva (A), Metamorph (B), recent Settler (C) of H. ionthas; Larva (D), Metamorph (E), late Metamorph (F) of* P. marmoreus. *These two species represent the extremes in development for the five species studied.*

Table 2. Summary information for five species of blenny from the northern Gulf of Mexico. Intervals (Larvae, Metamorphs, Settlers) were determined by clustering total character scores for a suite of 10 characters. Ontogenetic index = log SL/log L juv á 100, where SL is standard length of an individual and L juv is SL at the start of the juvenile stage. Total character score is the sum of scores assigned to the individual characters listed in Table 1. All sizes are mm SL. Statistics given are mean and (range).

Category	*Hypsoblennius invemar*	*Hypsoblennius ionthas*	*Hypleurochilus multifilis*	*Parablennius marmoreus*	*Scartella cristata*
Overall summary					
Sample size	55	41	42	50	30
Size range	5.4–18.3	5.0–17.5	5.3–18.3	5.8–21.5	5.8–18.0
Range of ontogenetic index	58.5–100.7	56.8–101.0	57.4–100.0	50.7–88.5 [1]	60.6–100.0
Range of total character score	1–41	1–41	1–41	1–37 [1]	1–42 [2]
Larvae					
Sample size	9	8	6	14	5
Size	9.7 (8.2–11.0)	8.0 (7.0–9.1)	8.9 (8.0–11.0)	14.2 (12.2–16.0)	7.9 (6.8–9.5)
Ontogenetic index	78.4 (72.9–81.2)	73.3 (68.7–77.9)	75.1(71.5–82.5)	76.4 (72.2–80.0)	71.3 (66.3–77.9)
Total character score	9.2 (6.0–13.0)	6.8 (4.0–9.0)	7.7 (6.0–12.0)	9.7 (7.0–11.0)	7. 0 (6.0–9.0)
Metamorphs					
Sample size	19	18	19	19	6
Size	12.3 (11.0–13.5)	10.7 (9.7–11.5)	12.5 (11.5–13.8)	19.5 (17.0–21.5)	10.6 (10.2–11.0)
Ontogenetic index	86.9 (83.1–90.2)	83.5 (80.2–86.2)	86.9 (84.0–90.3)	85.6 (81.8–88.5)	81.7 (80.3–83.0)
Total character score	19.7 (16–27)	14.9 (12–18)	19.5 (15.0–24.0)	20.8 (15–30)	21.0 (16–25)
Size range [3]	12.7 (12.0–13.5)	11.3 (11.0–11.5)	12.9 (12.2–13.8)	20.9 (20.5–21.5)	10.6 (10.2–11.0)
Ontogenetic index [3]	88.1 (86.1–90.2)	85.6 (84.6–86.2)	87.8 (86.1–90.3)	87.7 (85.7–88.5)	81.5 (80.3–83.0)
Total character score [3]	23.2 (22–27)	17.2 (16–18)	26.4 (23–31)	21.8 (19–24)	22.0 (19–25)
Settlers					
Sample size	18	8	14	9	17
Size [4]	12.2 (11.8–12.8)	12.1 (11.7–12.7)	12.1 (11.8–12.3)	19.3 (19.0–19.5)	11.3 (11.0–11.5)
Ontogenetic index [4]	86.7 (85.6–88.4)	87.9 (86.8–89.7)	85.8 (84.9–86.3)	86.0 (85.5–86.5)	84.0 (83.0–84.5)
Total character score [4]	27.3 (25–32)	32.7 (30–38)	34.0 (31–36)	37.0 (37–37)	29.3 (27–33)
Size at juvenile (L_{juv}) [5]	17.9	17.0	18.3	31.2 [6]	18. 0

[1] Low upper range of ontogenetic index and total character score is the result of not having collected specimens with bifurcate caudal fin rays (i.e., juveniles)
[2] Only *Scartella cristata* have nuchal cirri
[3] Three largest Metamorphs
[4] Three smallest Settlers
[5] Size at initial bifurcation of any primary caudal ray
[6] Estimated size at initial bifurcation of any primary caudal ray

Table 3. Canonical root means used to discriminate intervals of development for the pooled data set of five species of blenny from the northern Gulf of Mexico. Distance between means is a measure of how clearly discriminant functions separate intervals. Compare sign of each root with characters in Table 4 to determine which characters are associated with each interval. The developmental interval most clearly separated by a given root is in bold.

Interval of development	Numbers of specimens	Size range (mm SL)	Root 1	Root 2
Larvae	42	6.8–16.0	– 4.283	– 1.154
Metamorphs	82	9.7–21.5	– 0.206	**1.013**
Settlers	64	11.0–20.5	**6.410**	– 0.978

Root 1 discriminated Settlers from Metamorphs and Larvae, and root 2 separated Metamorphs from the other two intervals (Fig. 1B). State of orbital cirrus and fin development, number of teeth, and body pigmentation pattern provided most of the power to discriminate intervals in these blennies.

Larvae of all five species had 10 or fewer fang-like or conical teeth along each jaw, lacked pigment laterally on the trunk, and most lacked the ocular cirrus (if developing, then nub-like and unpigmented). Early Metamorphs had 12 to 14 incisiform teeth along each jaw; filamentous, unpigmented orbital cirri; and epidermal pigment on the trunk immediately behind the nape. Pigment behind the nape initiated formation of the first trunk band. *Parablennius marmoreus* had a somewhat different pattern of body and fin pigmentation (Fig. 2). Whereas presettlers of the other four species of blenny had moderately to heavily pigmented pectoral fins, *P. marmoreus* lacked pectoral fin pigment until just before settlement. In addition, late Larvae had a single melanophore along the dorsal midline of the caudal peduncle behind the last pterygiophore at about 14.0-mm SL (Fig. 2E). Melanophores were added along the dorsal midline in an anterior direction and reached the nape in late Metamorphs. Thereafter, bands of pigment formed along the trunk (Fig. 2F). Consolidation of pigment into bands, pigmentation of the orbital cirrus, the presence of 16-18 teeth, and formation of the nasal cirrus signaled approaching settlement in all five species of blenny. Recent Settlers had multiply furcated orbital cirri, a full complement of well-developed elements in all fins, typically 18 or more teeth, and a mottled pigmentation pattern.

Discussion

Assigning discrete character scores to individual ontogenetic events identified three natural intervals of development in these five blennies. Settlers had higher dorsal/anal ray and orbital cirrus scores than Metamorphs, and Metamorphs had higher trunk pigmentation, dorsal/anal ray, orbital cirrus, and dentition scores than Larvae (Tables 3 and 4). While changes in pigmentation may permit rapid and reasonably accurate determination of developmental intervals for large numbers of specimens with little manipulation, the use of general (i.e., non-specific) pigmentation patterns combined with other ontogenetic characters will provide better resolution in interval discrimination than pigment alone. Pigmentation patterns are genetically determined and among the most useful characteristics of fish taxonomy (Kendall et al. 1984), but are subject to preservation problems associated with bleaching and melanophore contraction. Consequently, the use of general but quantifiable patterns would minimize problems associated with the presence/absence of specific melanophores. Although convergent patterns can limit the usefulness of pigment in systematic studies (Kendall et al. 1984), this same commonality in pigmentation is valuable for interval discrimination.

Behavioral changes, such as settlement in blennies (Ditty 2002), and the initiation of schooling in some clupeids (Noakes and Godin 1988) and carangids (Masuda and Tsukamoto 1999) often coincide with changes in relative growth. Quantification of shape change based on body depth to body length ratios (Leis and Carson-Ewart 2000) or allometric methods (van Snik et al. 1997;

Table 4. Standardized canonical coefficients from a Discriminant Function Analysis of the species-pooled data set of 10 ontogenetic characters to identify which characters delimit intervals of development in five species of blenny from the northern Gulf of Mexico. Coefficients identify the interspecific suite of characters that best delimit intervals of development and represent the magnitude of each variable's contribution to that root. Compare sign of each character with roots on Table 3 to determine which characters are associated with each interval. Characters that provide the best discrimination are in bold.

Character	Root 1	Root 2
Preopercular spine	−0.047	0.042
Orbital cirrus	**0.399**	**0.451**
Nasal cirrus	0.058	0.075
Number of teeth	0.067	**0.601**
Dorsal/anal rays	**0.580**	**−0.576**
Pectoral fin	−0.025	−0.040
Pelvic pigmentation	−0.099	−0.201
Caudal fin	0.256	0.125
Body pigmentation	0.057	**−0.594**
Lateral line	0.361	0.294

Gisbert 1999; Neuman and Able 2002; Ditty 2002) may help delimit at least some intervals of development. In fact, changes in shape often occur at discontinuities, such as metamorphosis (Emerson and Bramble 1993) and the onset of the juvenile stage (Copp and Kovac 1996; Vilizzi and Walker 1999).

Lack of guidelines for character selection has made it difficult to choose a uniform suite of characters to develop a universal staging system, a problem magnified for blennies and other fishes that have relatively little spination (other than preopercular spines) and few obvious external characters. Traditionally, SL at complete formation of all median fin rays, at initial squamation, or size at settlement has defined the beginning of the juvenile stage, L_{juv} (Fuiman 1994), although Fuiman (1997) has suggested more recently that squamation should be complete. Reliance on a single character, such as initial or complete squamation, to determine when the juvenile stage begins as has been proposed, creates problems in scaleless fishes, such as blennies, and in fishes (swordfish, squirrelfish, tilefish, and anthiinae serranids) that complete scale development while still considered larvae (Kendall 1979; Potthoff and Kelley 1982; Leis and Carson-Ewart 2000).

Some types of characters are more difficult to evaluate than others are. Incorporation of behavioral characters into a staging system necessitates live material, a requirement not easily met. Similarly, clearing and staining to observe structural development is labor intensive and requires a large number of specimens to establish patterns of ossification (Potthoff 1984). In addition, progressive and continuous changes in ossification are more difficult to quantify than characters that exhibit a distinct ontogenetic change. Monitoring changes in body shape, scoring discrete ontogenetic events, such as segmentation of fin rays, and the use of general pigmentation patterns are more-practical criteria, although quality of pigmentation is subject to various preservation related problems. We encourage the assessment of a variety of characters (i.e., morphological, behavioral, physiological, pigmentation, etc.) to delineate intervals, when possible, because the number of characters can influence the likelihood that intervals coincide with any natural process or impor-

Table 5. A standardized procedure to determine 'natural' intervals of development in the early life of fishes.

Steps:

1) Select character set to examine
2) Assign scores to individual character states (each change in state represents an ontogenetic event)
3) Dip specimen in a solution of Cyanine Blue 5R (Acid Blue 113) to enchance anatomical contrast
4) Score individual characters and calculate a total character score for each specimen
5) Select linkage and distance rules, then submit total character scores to a clustering program
6) Review resultant tree diagram and determine the minimum linkage distance that separates clusters
7) Determine the number of clusters and submit data to a bootstrap resampling procedure to test cluster stability [1]
8) If clusters are stable, assign a desciptive label to each interval
9) Assign individuals to their interval of development
10) Run a Discriminant Function Analysis on the species-pooled suite of scores for the characters examined to determine the interspecific criteria that best delineates intervals
11) Formulate an ontogenetic index to scale data (for interspecific comparisons)[2]
12) Calculate basic statistics to summarize data

[1] DePatta Pillar (1999)

[2] Fuiman (1994)

tant function (Crowley 2000). A large number of characters will improve the resolution of patterns, while too few characters can impair pattern interpretation (Crowley 2000).

Evaluation of external characters to develop a staging system should provide information equivalent to that of internal characters, at least until all larva-specific characteristics are lost. The fact that all teleosts have fins and that patterns of fin development are generally familial (Kendall et al. 1984) encourages the use of fin ontogeny as a primary source of characters to develop an interspecific staging system. Dentition offers another reliable source of characters because most, but not all, teleosts have teeth. Species-specific characters (e.g., length of preopercular spines and when they are resorbed), however, must be eliminated from the suite of characters used to demarcate intervals, if the objective is interspecific comparison.

Our methodology (Table 5) reduces the subjectivity inherent in traditional staging systems and is robust, if characters typically considered qualitative (e.g., degree of pigmentation, body shape) are quantified carefully. Different patterns of pigmentation, as described here, can be quantified if analogous patterns are established 'a prior' for all species studied. As with any staging system, the researcher must make certain initial decisions about character selection and score assignment. Incorporation of the ontogenetic index into our methodology minimizes interspecific differences in size, given that size is not a reliable indictor of developmental state across taxa. Environmental factors can slow or interfere with developmental processes and induce differences in size at comparable states of development that confound interspecific comparisons (Dettlaff and Dettlaff 1961; Fuiman and Higgs 1997; Fuiman et al. 1998). In these five blennies, the coefficient of variation (CV) for size at settlement based on SL was taxon-dependent and ranged from 4.6% to 7.1%, but was 24.1% when taxa were combined (Ditty 2002). Employing the ontogenetic index to compare interspecific differences in size at settlement resulted in a CV for the index of 1.6%. The fact that the timing and progression of ontogeny is relatively stable within a species (Alberch et al. 1979; Alberch 1985) is an attribute that makes our ontogenetic approach ideal to discriminate intervals of development.

Improved methodologies for characterizing intervals of development have several advantages. For example, our procedure may permit evaluation of habitat quality because ecological disturbances that disrupt physiological processes can affect both the direction and extent of morphological transformations, thereby altering relative growth rates and the timing of ontogeny (Strauss and Fuiman 1985; Jacobsson et al. 1986). The methodology described here may also facilitate examination of differences in life-history strategies and habitat-use patterns that can promote identification of essential fish habitat and important nursery areas for fishery species (Lindeman et al. 1998; Lindeman and Synder 1999). In addition, if the number of late Metamorphs adequately represents the number of recent Settlers in examining abundance patterns (Schmitt and Holbrook 1999), monitoring the supply of the more easily sampled Metamorphs may allow better prediction of year-class strength (Bradford 1992). Although relationships between fisheries recruitment and stock size do not strengthen sufficiently to predict year-class strength until after settlement in demersal fishes (Bradford 1992), improved methods of estimating the number of potential recruits approaching settlement may increase predictive accuracy (Milicich et al. 1992; Thorrold 1992; Meekan et al. 1993). Better characterization of intervals may also permit evaluation of stage-specific mortality rates and provide a meaningful test of the concept of critical periods of development. Similarly, our methodology could be used to investigate ways to adjust the interpretation of shifts in otolith daily ring structure and improve information in that historical record.

In conclusion, scoring individual characters and summing character scores, combined with clustering techniques (either total scores or O_L values can be clustered), DFA, and statistical resampling procedures, as described here, provide a standardized and more objective methodology by which to characterize an individual's state of ontogeny and group individuals into comparable intervals. Categorization of individuals based on quantitative characters and objective treatment of characters facilitates evaluation and comparison of important ecological and early life history questions (Youson 1988). Assignment of character scores to discrete ontogenetic events, when combined with a dimensionless index of ontogeny, such as the O_L of Fuiman (1994), permits quantification of ontogeny, identification of the events that delimit developmental intervals, and interspecific comparisons. Our approach promotes recognition of intervals of development in preserved samples where it may be difficult to rely on pigmentation patterns and impossible to incorporate behavioral criteria. Elimination of species-specific characters and the diversity of teleosts and life-history patterns may prohibit development of a standardized staging system across higher taxonomic levels, although standardization at the family level appears possible.

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